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Carbohydrate accumulation and turgor maintenance in seedling shoots and roots of two boreal conifers subjected to water stress

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Water potential components and organic solutes were examined in shoots and roots of potted jack pine (*Pinus banksiana* Lamb.) and white spruce (*Picea glauca* (Moench) Voss) seedlings after exposure to 7 days of water stress. The osmotic potential at the turgor loss point ($\psi_{\pi TLP}$) decreased in shoots and roots of water-stressed seedlings of both species, resulting in the maintenance of positive turgor at lower xylem water potentials (ψ_x) compared with nonstressed seedlings. Following water stress, $\psi_{\pi TLP}$ of shoots and roots declined by 0.28 MPa and 0.14 MPa, respectively, in jack pine, and 0.19 MPa and 0.28 MPa, respectively, in white spruce. The osmotic potential at saturation ($\psi_{\pi 100}$) was significantly lower after water stress only in jack pine roots. Active osmotic adjustment during water stress was confirmed by higher concentrations of organic solutes in white spruce shoots (1.4× increase relative to nonstressed plants) and roots (1.7×) and in the roots (2.2×) but not the shoots of jack pine. Carbohydrates, particularly fructose and glucose, were the primary organic solutes accumulating in both species. Tissue elasticity was greater in the roots than the shoots of both jack pine and white spruce regardless of treatment. Consequently, the relative water content at the turgor loss point was 22% and 18% lower in the roots than in the shoots of jack pine and white spruce, respectively. Osmotic adjustment in the roots and shoots of these two boreal conifers suggests that preconditioning planting stock by exposure to water stress may increase carbohydrate concentrations and enhance seedling drought tolerance.

Key words: carbohydrate accumulation, drought tolerance, organic solutes, osmotic adjustment, *Picea glauca*, *Pinus banksiana*, water potential components.

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Les composantes du potentiel hydrique et les solutés organiques ont été examinés dans des tiges et des racines de pins gris (*Pinus banksiana* Lamb.) et d'épinette blanche (*Picea glauca* (Moench) Voss) cultivés en pot, après 7 jours d'exposition à un stress hydrique. Le potentiel osmotique au point de perte de turgescence ($\psi_{\pi TLP}$) diminue dans les tiges et les racines des plantules soumises au stress hydrique chez les deux espèces, ce qui conduit au maintient d'une turgescence positive au potentiel hydrique du xylème le plus faible (ψ_x) comparativement aux plantules non-stressées. À la suite d'un stress hydrique, la valeur ($\psi_{\pi TLP}$) des tiges et des racines diminue à environ 0,28 MPa et 0,14 MPa, respectivement, chez le pin gris, et 0,19 MPa et 0,28 MPa, respectivement chez l'épinette blanche. Le potentiel osmotique à saturation ($\psi_{\pi 100}$) est significativement plus faible après le stress hydrique, seulement chez les racines de pin gris. L'ajustement osmotique actif au cours du stress hydrique est confirmé par les fortes concentrations de solutés organiques chez les tiges d'épinette blanche (1,4× d'augmentation relativement aux plantes non-stressées) et les racines (1,7×) et dans les racines (2,2×) mais non dans les tiges du pin gris. Les glucides, en particulier le fructose et le glucose sont les solutés organiques primaires qui s'accumulent dans les deux espèces. L'élasticité des tissus est plus grande dans les racines que dans les tiges chez le pin gris aussi bien que chez l'épinette blanche indépendamment du traitement. Conséquemment, le contenu relatif en eau au point de perte de turgescence est de 22% et 18% plus bas dans les racines que dans les tiges du pin gris et de l'épinette blanche respectivement. L'ajustement osmotique dans les racines et les tiges de ces deux conifères de la région boréale suggère qu'un pré-conditionnement du matériel prêt à être planté, enl'exposant à un stress hydrique, pourrait augmenter les concentrations en glucides et à la fois augmenter la tolérance des plantules à la sécheresse.

Mots clés : accumulation de glucides, tolérance à la sécheresse, soluté organique, ajustement osmotique, *Picea glauca*, *Pinus banksiana*, composante du potentiel hydrique.

[Traduit par la rédaction]

Introduction

Jack pine (*Pinus banksiana* Lamb.) and white spruce (*Picea glauca* (Moench) Voss) seedlings are often planted on drought susceptible sites in the boreal forest region of North America where low soil water availability and high evaporative demand can create sustained plant water deficits. The ability of many plants to tolerate water stress is largely dependent on their capacity for osmotic adjustment, a mechanism that facilitates an osmotic gradient favourable for maintaining cell turgor through the accumulation of solutes (Hellebust 1976; Hsiao et al. 1976; Turner and Jones 1980; Morgan 1984). The turgor response to cellular water deficits is also affected by tissue

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elasticity, which determines the rate of decline in turgor pressure per unit loss in symplastic (i.e., osmotically active) water, and can have a passive effect on osmotic potential (Melkonian et al. 1982; Tyree and Jarvis 1982).

While cell osmotic and turgor properties have been studied in a number of woody plants (see reviews of Morgan 1984 and Abrams 1988), attention has largely centered on those properties in leaves or shoots. The root system may be an important site for osmotic adjustment (Greacen and Oh 1972; Hsiao and Acevedo 1974; Sharp and Davies 1979; Oosterhuis and Wullschleger 1987), but relatively little is known about the comparative ability of leaves and roots of woody plants to accumulate solutes and maintain turgor in response to water stress (Osonubi and Davies 1978; Kandiko et al. 1980; Pallardy et al. 1982; Parker and Pallardy 1985).

Osmotic adjustment in glycophytic agronomic species has been attributed predominantly to the accumulation of organic compounds, mostly soluble carbohydrates and to a lesser extent amino acids (Hellebust 1976; Morgan 1984). However, only limited information is available concerning the organic compounds that accumulate in woody plants as a consequence of water stress (Tschaplinski and Blake 1989).

In this study we compared the effects of water stress achieved by soil drying on tissue water relations and the organic solutes that accumulate in the shoots and roots of jack pine and white spruce seedlings.

Methods

Jack pine and white spruce seed was obtained from general northeastern Ontario collections. Both species were sown in Styroblock® No. 4 containers (cavity volume 65 cm^3, 160 cavities/block) and grown in a greenhouse under cultural practices similar to those described by Carlson (1983).

At 13 (jack pine) and 17 (white spruce) weeks after sowing, seedlings were transplanted into 600-cm^3 pots containing a 2:1 peat–vermiculite mixture, six seedlings per pot and 17 pots per treatment. Potted seedlings were allowed to acclimate in a growth room (16-h light, 30:22°C light:dark) for 1 week prior to treatment. The light intensity at plant height was 320 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of photosynthetically active radiation (PAR) supplied by super high output cool white (Westinghouse) and high output daylight (General Electric) fluorescent bulbs. Seedlings were exposed to either a water-stress treatment, achieved by soil drying, or to a nonstress treatment in which pots were watered daily. Jack pine and white spruce seedlings were treated separately in successive experiments. In the water-stress treatment soil drying was allowed to progress over a 7-day period, during which randomly arranged pots were rotated daily to assure uniform exposure to light and air movement. Prior to the start of the treatment period, pot weights were adjusted to within 0.5 g by the removal or addition of peat moss. Predawn xylem water potential (ψ_{XPD}) was measured on 6 to 10 water-stressed and nonstressed seedlings with a pressure chamber on alternate days during the soil drying period.

Pressure–volume analysis

Components of tissue water potential were estimated from pressure–volume analysis. At the end of the treatment period, pots containing water-stressed and nonstressed seedlings were watered to saturation and covered with plastic bags overnight. The next morning, seedling roots with shoots attached were carefully extracted and washed free of potting medium and then wrapped in moist paper towels and placed in sealed plastic bags for a second night. The time required for seedling preparation resulted in a rehydration period 1 day longer than the overnight rehydration period normally employed in pressure–volume analysis. It is unlikely that much osmotic deadjustment occurred during this period because other work with water-stressed black spruce (*Picea mariana* (Mill.) B.S.P.) seedlings found no loss of osmotic adjustment in shoots or roots 1 week after rewatering (R. S. Koppenaal, unpublished data). Similarly, Wilson and Ludlow (1983) found osmotic potentials in leaves of water-stressed buffel grass (*Cenchrus ciliaris*) had not returned to nonstressed levels 18 days after rewatering.

Pressure–volume curves were constructed from shoots and roots of seedlings following rehydration using a composite of 17 to 24 seedlings for each curve as described by Colombo (1987). Shoots were severed at the hypocotyl and the initial saturated weight recorded. Shoots were allowed to air dry on a laboratory bench until they reached a target estimated relative water content (RWC) at which time the xylem water potential (ψ_X) was measured once in a pressure chamber (PMS Instrument Co.) and the shoot weight recorded. Thus, each shoot yielded a single point of reciprocal ψ_X plotted against RWC, which when graphed together resulted in a composite pressure–volume curve. The composite pressure–volume technique is identical to that described by Hinckley *et al.* (1980), except that with the latter technique the balance pressure of a single shoot is measured repeatedly over the range of RWC to generate a pressure–volume curve. The pressure–volume curves presented in this paper are fitted to a composite of measurements from numerous seedlings, incorporating the genetic variation of the population sampled. The coefficient of determination associated with the linear regression between reciprocal ψ_X and RWC below the turgor loss point ranged from 0.78 to 0.96 for the composite pressure–volume curves obtained in this study (Table 1).

Roots from the same seedlings used for shoot pressure—volume analysis were treated in the same manner as shoots with one notable exception. To slow their rapid rate of water loss roots were dipped in a 20% (v:v) solution of Vapor Gard®, a commercial antitranspirant. Root weight was measured before and after dipping in Vapor Gard®. After removing excess Vapor Gard®, a transparent film of the substance remained adhered to the roots that accounted for approximately a 1% increase in root weight.

Percent relative water content of shoots and roots was calculated as

$$[1] \qquad RWC = \frac{PDW - DW}{TW - DW} \times 100$$

where TW is turgid weight, PDW is partially dehydrated weight, and DW is oven-dry weight (48 h at 90°C). The ψ_X of the shoots measured immediately after rehydration was slightly negative, (−0.07 to −0.2 MPa), indicating that they had not fully rehydrated in the theoretical sense where $\psi_X = 0$, a condition typically not attainable using pressure–volume techniques (Kandiko et al. 1980; Ritchie and Shula 1984). This anomaly was corrected by extrapolating the line of xylem water potential versus RWC to 0 MPa, which was then assigned a value of 100% RWC.

In roots of white spruce, ψ_X remained near zero as RWC fell to as low as 70%. Ritchie and Shula (1984) observed that ψ_X in Douglas-fir roots stayed near zero down to very low RWCs and suggested this anomaly resulted from the loss of apoplastic water absorbed during root soaking in preparation for generating pressure–volume curves. In this experiment, roots were soaked in water-saturated paper towels prior to pressure–volume analysis. For white spruce roots in particular, the loss of relatively large amounts of apoplastic water would account for constant ψ_X while RWC declined. To discount this absorbed, nonsymplastic water, 100% RWC was taken to be coincident with the point at which ψ_X initially decreased. Following the initial decline in ψ_X, the apoplastic fraction was assumed to be constant. Only slight adjustment was necessary in pressure–volume curves generated from jack pine roots.

Osmotic potential at full turgor ($\psi_{\pi_{100}}$) was estimated from the y-intercept of the linear regression between reciprocal ψ_X and RWC below the turgor loss point. The curvilinear part of the pressure–volume curve was fitted by hand. Osmotic potential at the turgor loss point ($\psi_{\pi TLP}$) and relative water content at the turgor loss point (RWC_{TLP}) were estimated at the point where the curvilinear and linear

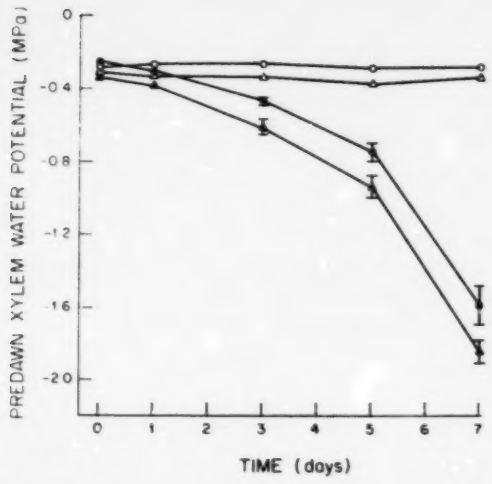

FIG. 1. The predawn xylem water potential of water-stressed (solid symbols) and nonstressed (open symbols) jack pine (△, ▲) and white spruce, (○, ●) seedlings over a 7-days period during which water was added only to pots of nonstressed seedlings.

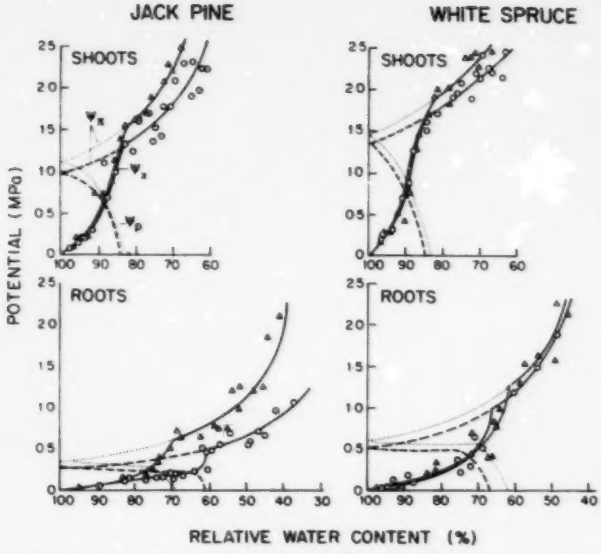

FIG. 2. Höffler diagrams showing water potential components of shoots and roots of jack pine and white spruce seedlings over the range of relative water content. A solid line is fitted through total xylem water potential measurements of water-stressed (△) and nonstressed (○) seedlings. Each point represents an individual shoot or root measurement. Osmotic and turgor potentials of stressed (....) and nonstressed (----) seedlings were derived from the fitted line of total xylem water potential. Turgor potential is positive whereas osmotic and water potentials are negative.

regions join. Symplast volume was estimated by extrapolation of the linear part of the pressure–volume curve to the x-axis. Turgor potential (ψ_p) was calculated as the difference between values taken from the hand fitted line of ψ_x as plotted on a Höffler diagram and the extrapolated values of ψ_π at RWCs within the curvilinear portion of the pressure–volume curve (where $\psi_p > 0$) (Cheung et al. 1975). Thus, calculations of ψ_p and ψ_π represent average population values as opposed to ψ_x that was directly measured on shoots and roots of several seedlings.

The weight averaged bulk modulus of elasticity ($\bar{\epsilon}$) is defined as the change in turgor pressure for a given fractional change in symplastic water content (Tyree and Jarvis 1982). Therefore,

$$[2] \qquad \bar{\epsilon} = \frac{d\,\psi_P}{d\,W_S} \times W_S$$

where W_S is the weight of symplasmic water (Tyree 1981). This allowed determination of the maximum bulk modulus of elasticity ($\bar{\epsilon}_{max}$) (tissues are least elastic) that has been shown in some cases to occur other than at full turgor (Colombo 1987).

Organic solute analysis

Seedlings were harvested for organic solute analysis at the same time as those sampled for pressure–volume analysis. Roots and shoots of six water-stressed and nonstressed seedlings were separated, frozen in liquid nitrogen, freeze dried for 48 h, and ground in a Wiley mill (20 mesh screen). Root (30 mg) and shoot (100 mg) samples were each subjected to two successive hot water extracts (60–70°) that were combined and freeze dried, followed by silylation with Tri-Sil Z (Pierce Chemical Co., Rockford, IL) to produce trimethylsilyl-(TMS-) organic solutes. TMS-derivated organic solutes of white spruce samples were partitioned with a 180 cm × 2 mm i.d. stainless steel column containing 5% SE-30 on 80/100 chromosorb W (Supelco Inc., Bellefonte, PA) in a Perkin Elmer 3920 gas chromatograph (Perkin Elmer Inc., Norwalk, CT). The TMS-derivatized organic solutes of jack pine were separated with a 180 cm × 4 mm i.d. glass column containing 2% SE-30 on 80/100 mesh Chromosorb W (HP) in a Varian 3700 gas chromatograph (Varian Inc., Sunnyvale, CA). The temperature was programmed to increase from 150°C, after a 4 min hold, at 8°C/min to a maximum of 275°C. The TMS-solutes were detected by a flame ionization detector (FID). Peaks were quantified with a Hewlett-Packard 3390A reporting integrator (Hewlett-Packard Co., Corvallis, OR) following injection of external standards. Unidentified compounds were quantified in fructose equivalents. Argon was used as the carrier gas with a flow rate of 30 mL/min. The flow rates for air and hydrogen for the FID were 300 and 30 mL/min, respectively. Injector and FID temperatures were 210 and 275°C, respectively. The identity of all compounds analyzed was confirmed by gas chromatography – mass spectrometry (GCMS). Representative shoot and root extracts containing water-soluble carbohydrates and other organic solutes were silylated as described above and injected into a Hewlett-Packard 5985 GCMS fitted with a DB5 capillary column (30 m × 0.25 μm). The separation of compounds with a DB5 capillary column is similar to the SE-30 packed column except the resolution is greater with the former. Column temperature was programmed to start at 100°C (held for 4 min), increasing at 4°C/min up to 230°C. Electron ionization with an electron impact of 70 eV was used to ionize the compounds.

Data analysis

Differences in osmotic potential between water-stressed and nonstressed seedlings at their saturation and turgor loss points were compared by analysis of covariance (SAS Institute 1988), using relative water content as the covariate. The model accounts for variation in mean response due to treatment as well as the value of the covariate and was applied to measurements in the region where reciprocal xylem water potential is linearly related to relative water content. The same technique was used to compare the relative water content at the turgor loss point of stressed and nonstressed seedlings using reciprocal xylem water potential as the covariate. Treatment differences in organic solute concentrations were analyzed using Student's t-tests. Data were transformed to natural logarithms when variances were not equal.

Results and discussion

Water potential components

Water stress developed at a similar rate in both jack pine and white spruce over the 7-day stress period, with little change in

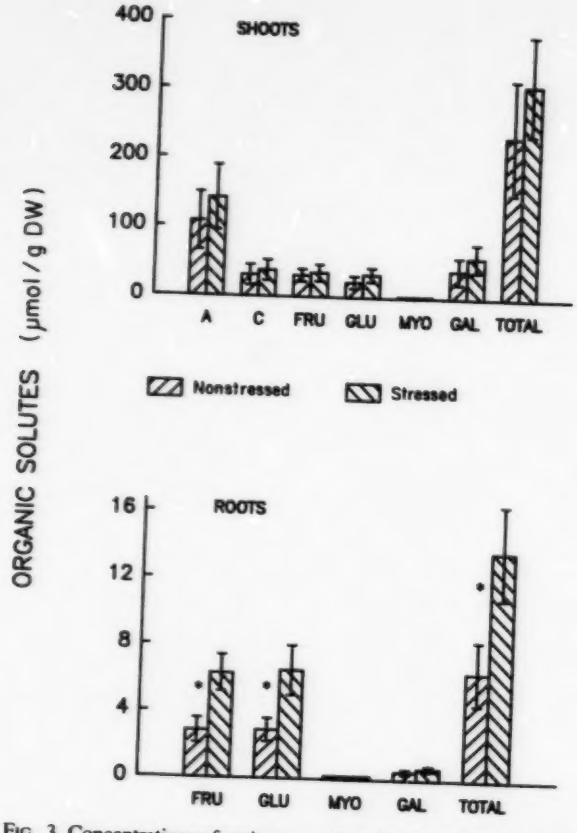

FIG. 3. Concentrations of various organic solutes in shoots and roots of water-stressed and nonstressed jack pine seedlings. Total organic solutes include both carbohydrates and unidentified organic solutes. A and C represent unidentified compounds. FRU, fructose; GLU, glucose; MY0, myo-inositol; GAL, galactose; TOTAL, total organic solutes. Values are means of six plants. Asterisks indicate significant differences ($P < 0.05$) between stressed and nonstressed seedlings. Vertical bars indicate the standard error of the mean.

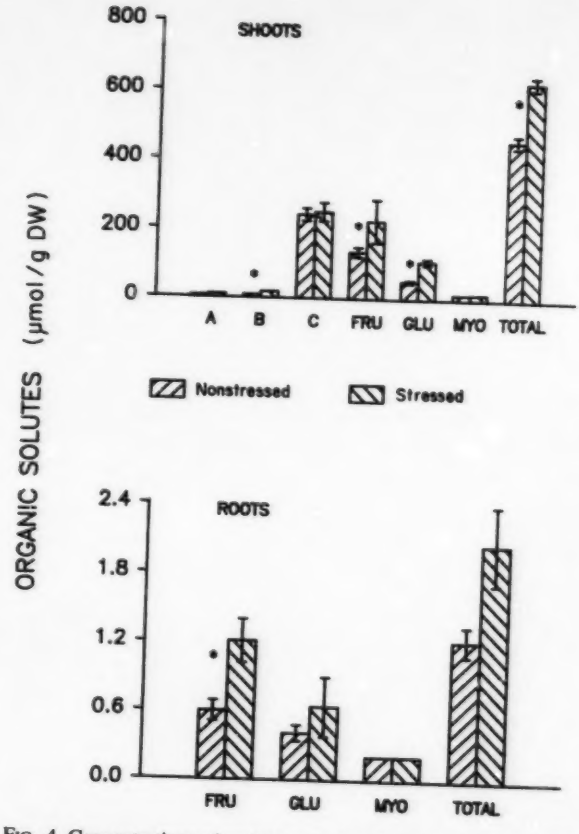

FIG. 4. Concentrations of various organic solutes in shoots and roots of water-stressed and nonstressed white spruce seedlings. A, B, and C represent unidentified compounds. Total organic solutes include both carbohydrates and unidentified organic solutes. Abbreviations as in Fig. 3. Data are means of six plants. Asterisks indicate significant differences ($P < 0.05$) between stressed and nonstressed seedlings. Vertical bars indicate the standard error of the mean.

predawn xylem water potential (ψ_{XPD}) until the 3rd day of stress, after which ψ_{XPD} declined at a more rapid rate, falling to -1.84 MPa in jack pine and to -1.59 MPa in white spruce by the last day of water stress (Fig. 1). While it has been demonstrated that osmotic adjustment is enhanced by the slow development of water stress (Jones and Rawson 1979; Levitt 1985), the relatively rapid rate at which ψ_{XPD} declined in this study, up to 0.45 MPa/day during the last 2 days of water stress, was sufficient to induce osmotic adjustment in shoots and roots of jack pine and white spruce (Table 1). This is consistent with the findings of Jones and Rawson (1979) that showed rates of water stress up to 0.7 MPa/day did not have a diminshed effect on osmotic adjustment in sorghum leaves.

Osmotic potentials at the turgor loss point in the shoots and roots of both jack pine and white spruce were lower in water-stressed seedlings (Table 1, Fig. 2). Osmotic adjustments at the turgor loss point in jack pine was 0.28 MPa and 0.14 MPa for shoots and roots, respectively, although proportionately the decline was approximately equal. In white spruce, water stress resulted in $\psi_{\pi TLP}$ decreasing more in roots (0.28 MPa) than in shoots (0.19 MPa) despite a more negative $\psi_{\pi TLP}$ in the shoots. Although water stress reduced the osmotic potential at full turgor by 0.09 MPa in jack pine roots, no significant decrease in $\psi_{\pi 100}$ occurred in jack pine shoots or white shoots and roots. While a lower $\psi_{\pi TLP}$ in the absence of lower $\psi_{\pi 100}$ has been interpreted as being indicative of increased tissue elasticity causing a passive decrease in osmotic potential (Davies and Lakso 1979; Parker and Pallardy 1985), the accumulation of organic solutes in tissue at full turgor (Figs. 3 and 4) indicates that active osmotic adjustment did occur. Failure to detect statistically significant differences in $\psi_{\pi 100}$ between stressed and nonstressed seedlings may have been a function of the distribution of pressure–volume measurements in relation to $\psi_{\pi 100}$ and $\psi_{\pi TLP}$ (which were extrapolated by linear regression). The estimate of $\psi_{\pi 100}$ had a larger error component associated with it since it was further away from the measured pressure–volume points on the regression line than $\psi_{\pi TLP}$.

A larger osmotic gradient for the movement of water across cell membranes allowed water-stressed jack pine and white spruce to maintain higher ψ_P in shoots and roots at all values of ψ_X (Fig. 2), although the roots of nonstressed jack pine seedlings maintained positive turgor to a slightly lower RWC than the roots of stressed seedlings. Buxton et al. (1985) also found osmotic adjustment in 22-week-old jack pine and white spruce seedling shoots following a period of moisture stress.

TABLE 1. Summary of pressure–volume analyses of shoots and roots of jack pine and white spruce seedlings with and without water stress

	Jack pine						White spruce					
	Shoots			Roots			Shoots			Roots		
	Stressed	Non-stressed	*p* value	Stressed	Non-stressed	*p* value	Stressed	Non-stressed	*p* value	Stressed	Non-stressed	*p* value
$\psi_{\pi 100}$ (MPa)	−1.10	−0.95	0.104	−0.35	−0.26	0.018*	−1.45	−1.34	0.449	−0.62	−0.51	0.307
$\psi_{\pi TLP}$ (MPa)	−1.56	−1.28	0.0004*	−0.62	−0.48	0.0006*	−1.87	−1.68	0.034*	−1.27	−0.99	0.207*
RWC_{TLP} (%)	82.0	83.0	0.820	69.0	61.0	0.004*	83.3	84.5	0.837	62.0	66.8	0.190
ϵ_{max} (MPa)	6.79	9.00	—	3.44	12.75	—	10.63	11.19	—	6.18	6.16	—
r^2	0.95	0.81	—	0.93	0.80	—	0.87	0.78	—	0.83	0.96	—

NOTE: The *p* value of the difference between water stressed and nonstressed values within the same species and plant component was determined by analysis of covariance of the reciprocal xylem water potential versus relative water content relationships. The r^2 value is the coefficient of determination of the linear regression between reciprocal ψ_X and RWC below the turgor loss point ($\psi_p = 0$). *, significant at $P \leq 0.05$.

In their greenhouse study, shoot osmotic adjustment at full turgor was 0.47 and 0.16 MPa in jack pine and white spruce, respectively, after 6 days of soil drying. Grossnickle and Blake (1987) found seasonal osmotic adjustment in shoots of field-planted bare root white spruce but not in jack pine seedlings. They reported osmotic adjustment in white spruce shoots at saturation and the turgor loss point of 0.57 and 0.65 MPa, respectively. Our estimates of shoot $\psi_{\pi 100}$ and $\psi_{\pi TLP}$ for both species are similar to those reported by Grossnickle and Blake (1987) but were higher (less negative) than those measured by Buxton et al. (1985). Components of root water potential were not examined in either of these previous studies.

The relative capacity of shoots and roots to adjust osmotically varies among tree species, although relatively few studies have compared shoot and root water potential components in response to drought (Osonubi and Davies 1978; Kandiko et al. 1980; Park and Pallardy 1985, 1988). As in jack pine and white spruce, osmotic adjustment was observed in both the shoots (or leaves) and roots of *Tsuga heterophylla* (Raf.) (Sarg.) (Kandiko et al. 1980) and *Quercus stellata* Wong (Parker and Pallardy 1988). In seedlings of *Quercus robus* L. (Osonubi and Davies 1978) and *Juglans nigra* L. (Parker and Pallardy 1985), roots generally had a greater capacity for osmotic adjustment than the shoots or leaves, while the opposite was true of *Quercus alba* and *Q. macrocarpa* Michx. (Parker and Pallardy 1988) where osmotic adjustment occurred in the shoots but not the roots. A direct benefit of root turgor maintenance by osmotic adjustment may be sustained root growth into a larger soil volume with potentially more water available for seedling uptake (Greacen and Oh 1972; Sharp and Davies 1979), thus avoiding large perirhizal resistances that could develop when nongrowing roots deplete soil water at the soil–root interface (Faiz and Weatherley 1977; Herkelrath et al. 1977).

In discussing the role of root osmotic adjustment, Turner (1986) has suggested that low soil water content may override any turgor maintenance by the shoot, resulting in reduced stomatal conductance and photosynthesis, and that osmotic adjustment will only be effective in maintaining growth processes of the shoot under declining soil water contents if osmotic adjustment of the roots also occurs. Moreover, as soil water becomes less available, root osmotic adjustment may act to maintain the balance of phytohormones which regulate shoot growth (Turner 1986).

There were distinct differences in the turgor relationships between shoots and roots in both species. Roots displayed a much more gradual decline in ψ_p as RWC declined than did shoots (Fig. 2) where the decline was exponential, reflecting greater cell wall elasticity in the roots. Consequently, the RWC_{TLP} of jack pine and white spruce roots was much lower than in the shoots (Table 1). These inherent differences in the turgor relations of roots and shoots or leaves have also been observed in *Tsuga heterophylla* (Raf.) Sarg.) (Kandiko et al. 1980). *Pseudotsuga menziesii* (Mirb.) Franvo (Ritchie and Shula 1964, and *Pinus pinaster* Ait. (Nguyen and Lamant 1989).

Water stress did not alter tissue elasticity in white spruce shoots or roots (Table 1). In contrast, water stress may have reduced ϵ_{max} (increased tissue elasticity) in jack pine, particularly in the roots where a more gradual decline in ψ_p of stressed seedlings occurred when ψ_p dropped below about 0.15 MPa (Fig. 2), although there were very few ψ_X measurements in this region of ψ_p. A similar increase in tissue elasticity following drought was observed in roots of *Quercus alba* and *Q. macrocarpa* (Parker and Pallardy 1988). Turgor maintenance in jack pine may thus rely on both solute accumulation and increased root tissue elasticity, while spruce turgor maintenance is primarily the result of osmotic adjustment.

Osmotic potentials of shoots and roots were lower in white spruce than in jack pine (Table 1), which is in general agreement with the findings of Buxton et al. (1985). Although this indicates that white spruce is able to maintain positive turgor to lower water potentials than jack pine, the greater amount of new root growth produced by jack pine seedlings after outplanting (Grossnickle and Blake 1987) may allow that species to avoid the development of severe water deficits by extracting from a larger volume of soil.

Organic solute accumulation

Water stress induced an accumulation of carbohydrates in the roots of jack pine (Fig. 3) and in the roots and shoots of white spruce (Fig. 4). Although concentrations of organic solutes were variable in the shoots of both stressed and nonstressed jack pine seedlings, water stress induced a greater than 2-fold increase in fructose and glucose in the roots, resulting in a 2.2-fold difference in total organic solutes. Similarly, the concentration of fructose doubled in the roots of water-stressed white spruce, resulting in a 1.7-fold difference in total water-soluble carbohydrates between stressed and nonstressed seedlings. Water stress also resulted in an accumulation of fructose (1.7× relative to nonstressed plants), glucose (2.1×), and an unidentified compound B (2.0×) in the shoots of white spruce resulting in a 1.4-fold increase in total organic solutes. The bulk of the organic solutes in the roots and shoots of both jack pine and white spruce were monosaccharides, whereas sucrose levels were negligible. Since sucrose is a major photosynthate and transport compound in trees, it is likely that sucrose

demand was particularly high, with sucrose cleavage resulting in fructose accumulation in tissues in response to water stress.

In contrast to jack pine and white spruce, sucrose was the major osmotically active compound found in leaves of the hybrid poplar *Populus deltoides* Bartr. × *nigra* L. (DN 22) following water stress, although fructose and glucose were also accumulated (Tschaplinski and Blake 1989). A substantial degree of osmotic adjustment occurred in the leaves of *P. deltoides* (1.0 MPa), whereas there was no evidence of osmotic adjustment in the roots. In the present study osmotic adjustment, as indicated by organic solute concentrations, was clearly evident in the roots of both conifers as well as the shoots of white spruce.

This study demonstrates that the capacity to accumulate organic solutes varies by species and by tissue type. The accumulation of organic solutes, primarily in roots of jack pine and to a lesser extent in the shoots and roots of white spruce during a single drying cycle, suggests a capability to rapidly respond to water deficits. Such a capability contributes to the maintenance of turgor and the growth of roots under water deficits, and potentially greater exploitation of soil water reserves. Carbohydrate accumulation induced by preconditioning to water stress may increase drought tolerance and thereby improve field performance, as found in a subsequent study of field-planted jack pine seedlings (R. S. Koppenaal, unpublished data).

More research is required on the timing of solute accumulation in response to stress in different tissues, the source of solute accumulation, and the role of carbon reserves, carbon allocation, and partitioning in osmotic adjustment in tree species.

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